PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(3):447–456. 1997.

# *Lamellibrachia satsuma,* a new species of vestimentiferan worms (Annelida: Pogonophora) from a shallow hydrothermal vent in Kagoshima Bay, Japan

Tomoyuki Miura, Junzo Tsukahara, and Jun Hashimoto

(TM) Faculty of Fisheries, Kagoshima University, 4-0-20, Shimoarata, Kagoshima 890, (JT) Faculty of Sciences, Kagoshima University, 1-21-35, Korimoto, Kagoshima 890, and (JH) Japan Marine Science and Technology Center, 2-15, Natsushima, Yokosuka 237, Japan

*Abstract.*—Vestimentiferan tube worms were found forming clumps in 82–110 m in Kagoshima Bay, southern Japan, during a series of surveys exploring the biological community associated with shallow hydrothermal vents in 1993. The newly found tube worm is described here as *Lamellibrachia satsuma,* a new species. It differs from other congeneric species in having a short vestimentum, a short obturaculum, up to 4 pairs of lamellar sheaths and up to 19 pairs of branchial lamellar sheaths. About 20 living worms were maintained in a laboratory for more than 400 days. Release of eggs from the opening of the tube was observed at the beginning of the maintenance experiment. Trochophore-like larvae were also examined and photographed.

---

Kagoshima Bay is characterized by two gigantic calderas, the Aira and the Ata, which form the northern and the southern areas of the bay, respectively. The northern bay-head area is about 18 km long and 20 km wide and is separated from the southern area by an active volcano, Mt. Sakurajima, but connected by a shallow and narrow strait (40 m deep and 2 km wide). The eruption forming the Aira Caldera that is the present bay-head area is thought to have occurred about 22,000 years ago (Aramaki & Ui 1966). In the east part of the head area, two hydrothermal vent sites at depths of about 80 m and 200 m are recognized by the appearance of gas bubbles that reach the surface and are called "Tagiri" by local fishermen (Oki & Hayasaka 1978). The word "Tagiri" originates from a Japanese word meaning 'boil and bubble'. Although "Tagiri" sites are quite shallow when compared with other hydrothermal vents, the chemical characteristics of these sites are believed to be the same or close to those of hydrothermal vents where associated biological communities are found. In 1993, during a series of surveys exploring the community associated with submarine fumaroles in Kagoshima Bay, we discovered a world of vestimentiferan worms forming clumps at depths of 82–110 m and collected a batch of living worms by means of a small dredge attached to a deep towed camera system (Hashimoto et al. 1993).

The first vestimentiferan species, *Lamellibrachia barhami,* was described as a unique pogonophoran worm from the Northeast Pacific at a depth of 1125 m (Webb 1969). In a study of *L. luymesi* collected at 500 m depth off Guyana, the class Vestimentifera was placed in the phylum Annelida (van der Land & Nørrevang 1975). Jones (1985) proposed, however, a new phylum, Vestimentifera, for the vestimentiferan tube worms in working on above species and various other species from deep-sea vents and seeps. Mañe-Garzón & Montero (1985) also proposed a separate phylum under the name Mesoneurophora with the description of a new species of *Lamellibrachia.* Describing two new vestimentiferan species, Southward (1991)

reclassified the vestimentiferan worms as a subclass of the class Pogonophora within the phylum Annelida. The affiliation of vestimentiferans to Annelida is also suggested by the hemoglobin structure (Suzuki et al. 1989) and by the amino acid sequence of Elongation Factor-1α (Kojima et al. 1993), the analysis of 28S ribosomal DNA demonstrated that the Vestimentifera form a monophyletic group to the exclusion of the polychaete *Melinna* and the periviate pogonophore *Siboglinum* used for comparison (Williams et al. 1993). Rouse & Fauchald (1995) recently proposed that the name Articulata be used to include the Vestimentifera and Pogonophora as well as the Clitelata, the Polychaeta, and the Euarthropoda and Onychophora. In this study, we follow the classification proposed by Southward (1991) and place the vestimentiferan worms in the phylum Annelida.

To date, eight genera and 13 species of vestimentiferans have been described from hydrothermal vents, cold seeps, and other deep-sea bottoms (Jones 1985, Southward 1991, Southward & Galkin 1997). Two of them were amalgamated into a single species on the basis of careful examination of morphology and allozymes (Southward et al. 1995). Vestimentiferans are known from depths of 300–3270 m, in the eastern Pacific and the Gulf of Mexico (Jones 1985), the Lau Basin (Southward 1991), the Manus Basin (Southward & Galkin 1997), off Guyana (van der Land & Nørrevang 1975), off Uruguay (Mañe-Garzón & Montero 1986), and from the eastern Atlantic (Dando et al. 1992). Around Japan, several types of vestimentiferans have been also observed by manned or unmanned deep-sea submersibles and captured from deep-sea chemosynthetic communities in Sagami Bay (Hashimoto et al. 1989) and the mid-Okinawa Trough (Hashimoto et al. 1995) between depths of 690–1370 m in tectonically active zones. The vestimentiferans in Kagoshima Bay represent the shallowest occurrence of the group in the world. Recently, partial nucleotide sequences of mitochondrial DNA were analyzed from several local populations of Japanese vestimentiferans (Kojima et al. 1995). This analysis suggested the presence of more than one genetically distinguishable populations of *Lamellibrachia* species-complex around Japan. The authors also suggested that the populations differed in their vertical distribution. In this study, a shallow water species from Kagoshima Bay is described.

## Material and Methods

More than a hundred vestimentiferan specimens were collected by a small dredge 40 cm wide × 10 cm high × 50 cm deep, attached about 1 m beneath the bottom of a deep towed color television camera system operated by R/V *Kaiyo,* in the northern semi-closed area of Kagoshima Bay in February, 1993. Other additional specimens were collected by an unmanned deep-sea research vehicle *Dolphin 3K* seven months later, at the same site.

Specimens for taxonomic study were fixed in 10% formalin and transferred to 70% ethanol. Some dozens of worms were dissected from their tubes on the vessel and the remainder were kept intact. Specimens for chemical analysis were frozen at −80°C, a part of which were used in this study to calculate the dry/wet weight ratio of the soft body. Living worms were washed very carefully by using a brush to eliminate sediments and to examine newly settled larvae that might attach on the adult tubes. Every ten to twenty cleaned specimens were transferred into a 10-liter bottle and kept in the refrigerator of the research vessel at about 5°C. The living animals were transported to the laboratory of the Faculty of Fisheries at Kagoshima University within a week after the sampling. The worms were maintained in a glass tank 30 cm wide × 18 cm long × 24 cm deep filled with 10 l of filtered seawater (Millipore 1.2 μm filter). The tank was maintained at 16°C in an incubator because the temperature of the bottom seawater at the collecting site is constant

throughout the year at about this value. The water was changed for every 7–14 days to maintain a salinity of about 34 parts per thousand and a pH value of about 8.2, even though this last value altered by the addition of sodium sulfide. The worms were provided on average with 1.6 g of sodium sulfide ($Na_2S{\cdot}9H_2O$) as a source of hydrogen sulfide twice a day. The maximum concentration of hydrogen sulfide was calculated to be about 0.7 mM per 1 of sea water (not analyzed). The concentration in culture was, therefore, about 35 times higher than the concentration of hydrogen sulfide in the field, where only 0.02 mM per 1 was recorded.

The types are deposited in the National Science Museum, Tokyo (NSMT), Japan Marine Science and Technology Center (JAMSTEC), the National Museum of Natural History, Smithsonian Institution (USNM), the Los Angeles County Museum of Natural History (LACM-AHF), the Museum National d'Histoire Naturelle de Paris (MNHN), and the Australian Museum, Sydney (AM).

## Family Lamellibrachiidae Webb, 1969
## Genus *Lamellibrachia* Webb, 1969
## *Lamellibrachia satsuma,* new species
## Figs. 1–5

*Material examined.*—Holotype (NSMT-Pc-H3), 15 paratypes (5: NSMT-Pc-P4, P5, P6, P7, P8; 10: USNM 175102–175111), Kagoshima Bay, Deep Tow Camera Observation DT-13, 6 Feb 1993, 31°39.55′N, 130°48.07′E, 98 m; 13 paratypes (5: MNHN UE798–UE802, 8: JAMSTEC Ves-0270-77-93), DT-15, same site, 6 Feb 1993, 102 m; 6 paratypes (3: MNHN UE803–UE805, 3: JAMSTEC Ves-0278-80-93), *Dolphin 3K* Dive 154, 12 Sep 1993, 31°39.83′N, 130°48.97′E, 101 m; 40 paratypes (10: USNM 175092–175101; 10: LACM-AHF POLY 1873–POLY 1882; 10: AM W23599–W235608; 10: JAMSTEC Ves-0281-90-93), *Dolphin 3K* Dive 157, 12 Sep 1993, 31°39.80′N, 130°48.05′E, 122 m; 7 paratypes (JAMSTEC Ves-0291-97-93), *Dolphin 3K* Dive 164, 16 Sep 1993, 31°39.70′N, 130°48.02′E, 110 m.

*Measurements.*—Tube length 60–1000 mm ($\bar{X}$ 317 mm, $n$ = 71); opening width of top collar 2.5–8.7 mm ($\bar{X}$ 5.6 mm, $n$ = 78), bottom width of top collar 1.7–7.2 mm ($\bar{X}$ 3.9 mm, $n$ = 81), width of basal end 0.5–2.4 mm ($\bar{X}$ 1.1 mm, $n$ = 53); tube wet weight 0.18–4.16 g ($\bar{X}$ 1.35 g, $n$ = 53). Body length 45–443 mm ($\bar{X}$ 219 mm, $n$ = 53); body wet weight 0.08–1.57 g ($\bar{X}$ 0.68 g, $n$ = 53) (dry/wet weight ratio 0.06–0.28, $\bar{X}$ 0.23, $n$ = 37, measured differently using materials for chemical analysis). Obturacular length 1.8–9.8 mm ($\bar{X}$ 5.2 mm, $n$ = 64); obturacular width 1.0–5.6 mm ($\bar{X}$ 4.1 mm, $n$ = 53). Vestimental length 7.2–24.0 mm ($\bar{X}$ 17.2 mm, $n$ = 64). Vestimental length/Obturacular length ratio 2.1–8.3 ($\bar{X}$ 3.5, $n$ = 64); Vestimental length/obturacular width ratio 2.3–9.7 ($\bar{X}$ 4.5, $n$ = 53). Obturacular lamellar sheaths 0–4 pairs ($\bar{X}$ 2.77, $n$ = 57). Sex ratio 1.39:1 (32 males: 23 females).

*Description.*—Anterior face of obturaculum of adult bare, lacking secreted structures (Figs. 1a, b, 2a); with up to 19 pairs of branchial lamellae (Figs. 1a, b, 2a, b); each lamella formed by a single series of fused branchial filaments with pinnules; branchial lamellae hidden by up to four pairs of peripheral lamellar sheaths (Figs. 1a, b, 2a, b); sheaths composed of fused fine filaments, with only extreme distal tips of filaments free (Figs. 1a, b, 2a, b); obturaculum lenticular in transverse section (Fig. 2b), lacking dorsal groove, with ventral ridge, distally; with single, medial excretory pore opening in groove at base of obturaculum. Anterior margin of vestimentum forming short sheath or collar extending around base of obturaculum; central dorsal surface of vestimentum of male (holotype) with paired ciliated grooves, diverging at anterior ends (Fig. 1a); postero-ventral margin of vestimentum broadly incised (Fig. 1a, b); ventral surface with numerous small papillae topped by cuticular plaques 35–63

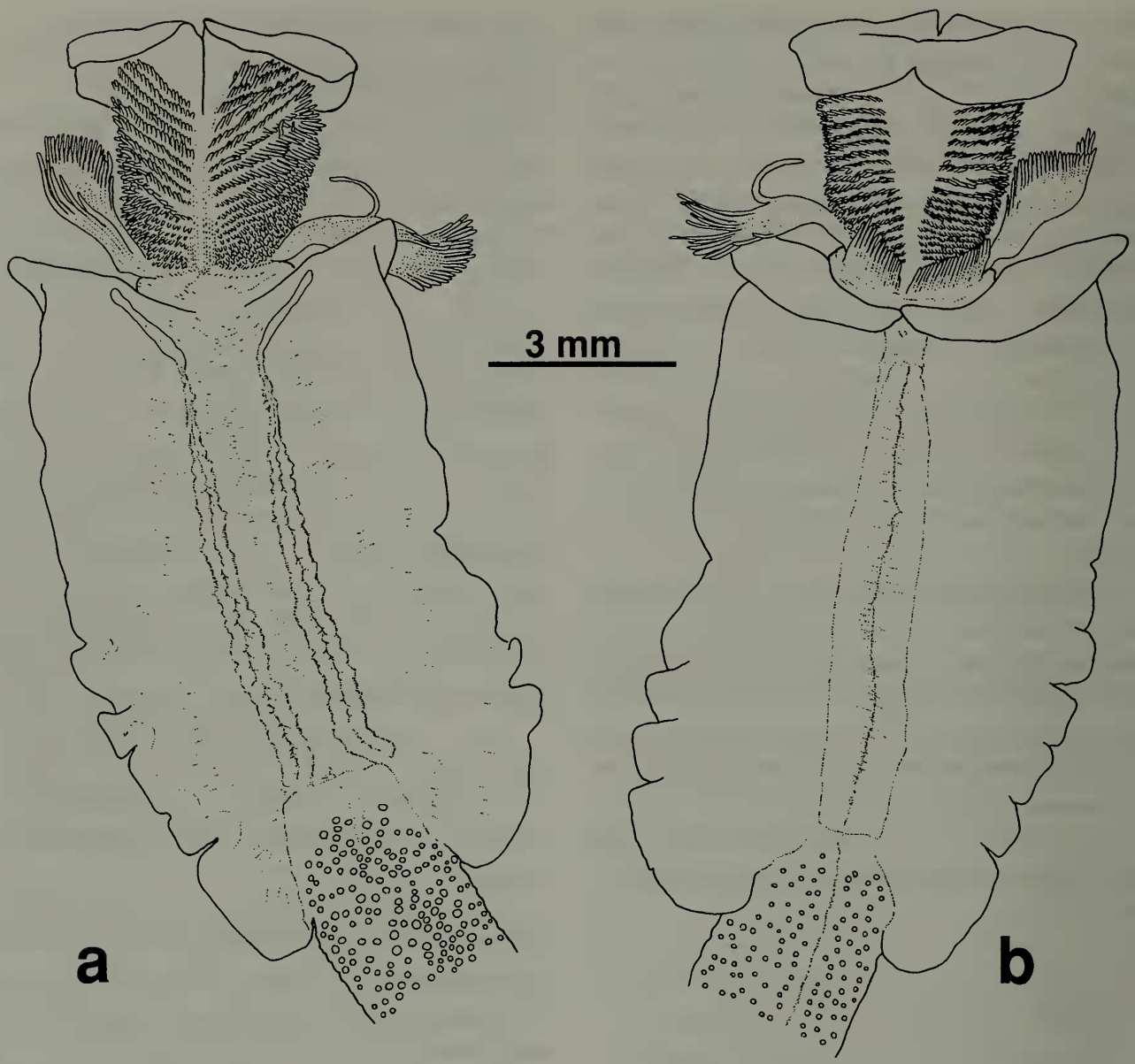


Fig. 1. *Lamellibrachia satsuma,* new species.—Holotype. a, Anterior end, in dorsal view; b, Same, in ventral view. Body fixed after removed from the tube. Scale = 3 mm.

μm in diameter. Trophosome very long, with numerous small papillae topped by cuticular plaques 51–82 μm in diameter. Opisthosome of selected specimen with 33 segments (Fig. 3a–c), anterior 27 with a single row of setae (Fig. 3b, d–f); most setae with two groups of denticles, anterior group bearing 6–9 denticles, posterior group with 10–15 denticles in 3–4 rows (Fig. 3e–f). Tube with obvious growth collars and irregularly placed light and dark bands (Figs. 2a, 4). Anterior parts of tubes more straight than posterior in large specimens; posterior parts coiled in general. Tubes tangled together in tight clusters, making large hemispherical clumps on thick sediments; clumps sometimes more than 10 m in diameter.

*Etymology.*—The specific epithet *satsuma,* a noun in apposition, refers to the old province on Kyushu island. Japanese name of the species, "satsuma-haorimushi" is also composed of the provincial name and the group name of vestimentiferan worms.

*Remarks.*—Among the five described species of the genus *Lamellibrachia, L. satsuma* and *L. barhami* Webb, 1969 differ from the other three by the number of peripheral lamellar sheaths, i.e. up to four pairs in the first two species, six pairs in *L.*

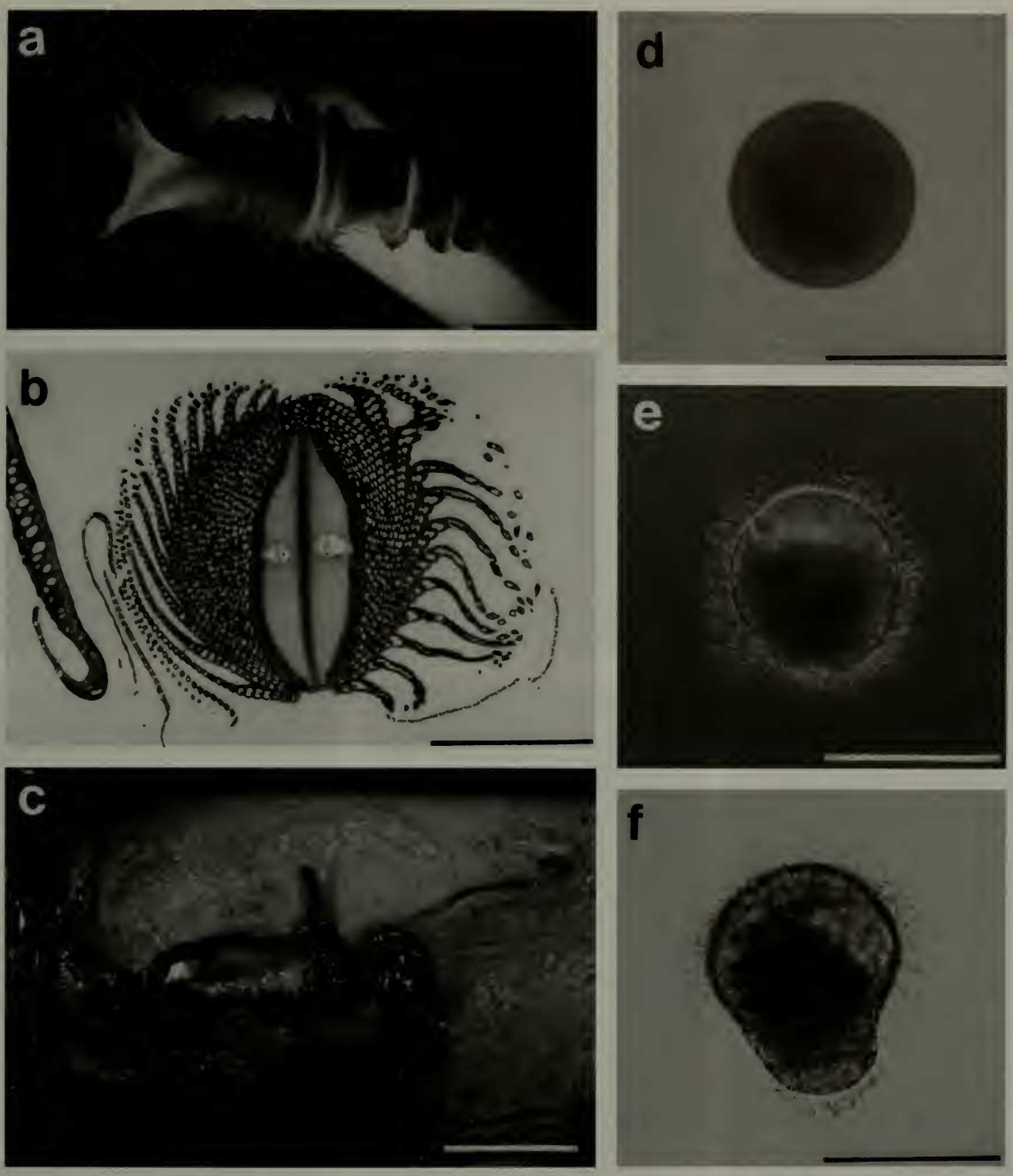


Fig. 2. Lab-reared specimens and embryos of *Lamellibrachia satsuma.*—a, Anterior end with the obturaculum, branchiae and the lamellar sheaths extending from the tube, scale = 3 mm; b, Transverse section near base of obturaculum, scale = 1 mm; c, Regenerated posterior ends of tubes attached to the glass bottle surface, scale = 10 mm; d, Released egg, scale = 0.1 mm; e, Trochophore-like larva about two-weeks old, in anterior view (upper hemisphere), scale = 0.1 mm; f, Same, in latero-posterior view (lower hemisphere with telotroch-like ciliated area), scale = 0.1 mm.

*luymesi* van der Land & Nørrevang, 1975, seven pairs in *L. victori* Mañe-Garzón & Montero, 1985, and 8–16 pairs in *L. columna* Southward, 1991. In *L. satsuma,* more than half of examined specimens has three to four pairs of lamellar sheaths, but only one or two pairs are large enough to cover the branchial region in most case. One very small specimens considered as a juvenile of *L. satsuma* has no lamellar

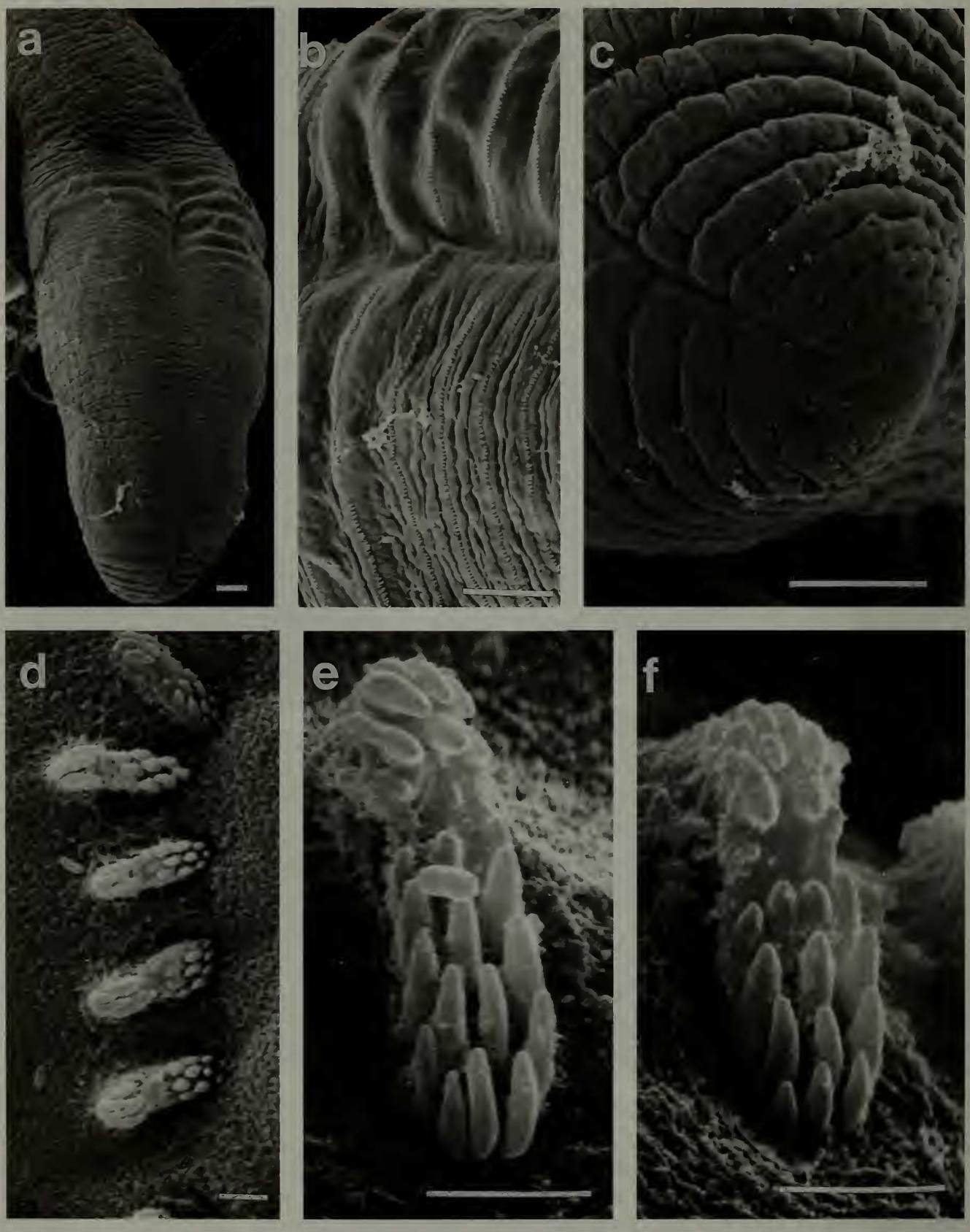


Fig. 3. *Lamellibrachia satsuma,* new species.—a, Regenerated opisthosome from a lab-reared specimen; b, Anterior portion of the same enlarged; c, Posterior portion of the same enlarged; d, Portion of opisthosome with a single row of setae; e, and f, Setae. Scale bars = 0.1 mm for a–c and 0.002 mm for d–f.

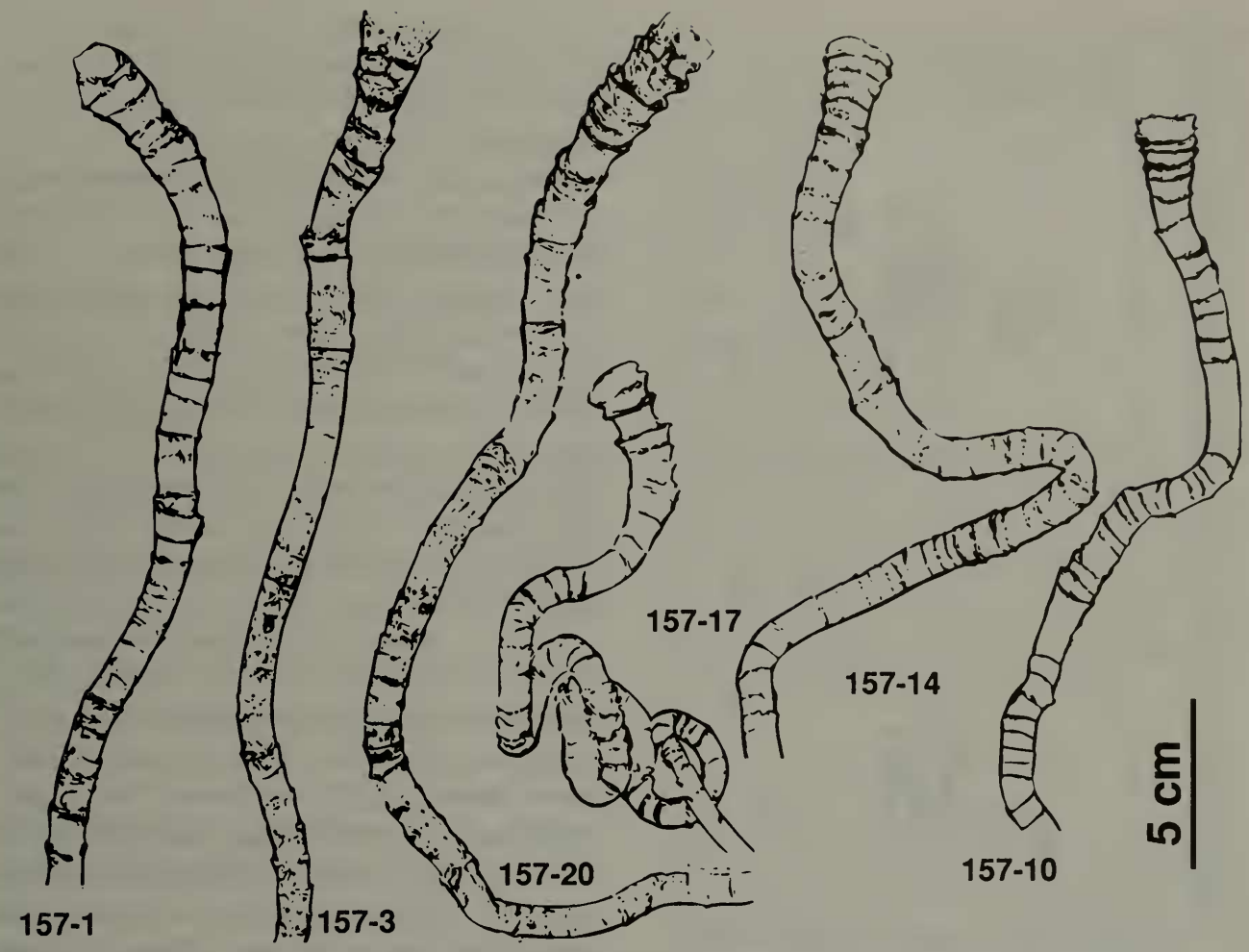


Fig. 4. *Lamellibrachia satsuma,* new species.—Anterior portion of tubes of selected paratypes.

sheaths. *Lamellibrachia satsuma* has up to 19 pairs of branchial lamellae; this number is smaller than in *L. barhami* which has as many as 25 pairs of branchial lamellae (Webb 1969; Jones 1985). The ratio of obturacular length to width ovewrlaps in these two species, but more variable in *L. barhami* (Fig. 5). *Lamellibrachia satsuma* is slightly smaller in size and has a shorter vestimentum and obturaculum (Fig. 5).

The diameter of cuticular plaques on the vestimentum and the trophosome are measured for *L. columna* (vestimental plaques 65–90 μm, trunk plaques 70–120 μm) and for *L. barhami* (60–115 μm, 115–160 μm, respectively) by Southward (1991, also her personal communication). These plaques are smaller in *L. satsuma* (35–63 μm, 51–82 μm, respectively) than the above two species.

The tube form is slightly different in *L. barhami* and *L. satsuma.* The tubes are twisted throughout the length in *L. barhami,* whereas the anterior parts of tubes are relatively straight in *L. satsuma. Lamellibrachia satsuma* forms very crowded clumps on the sediment and the tubes appear to be apart from one another in growing straightly (Fig. 2 in Hashimoto et al. 1993). These two species differ from each other also in their vertical and ecological distribution, i.e. *L. satsuma* lives in volcanic vents at depths of 98–110 m and perhaps also in cold seep sites of about 300 m depth, whereas *L. barhami* is presently known only in cold seep sites at depths of 1100–2000 m.

*Observation of living worms in laboratory.*—The worms extended the anterior part of their body from the tube, exposing the obturaculum and the lamellar sheaths (Fig. 2a). The anterior end was extended whether light was on or off, even when the strobe light was flashed. However, the

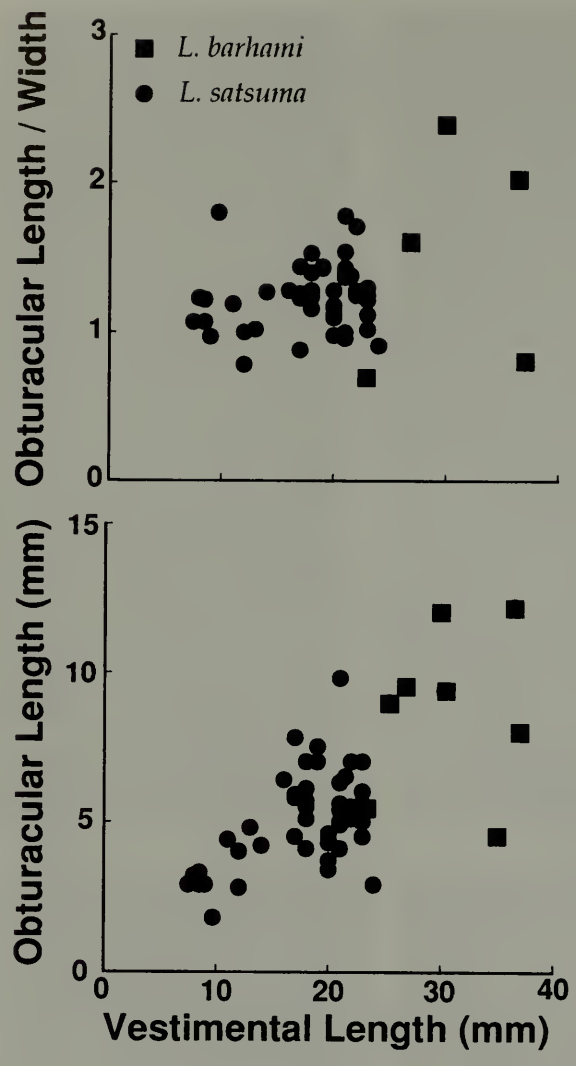


Fig. 5. Relationship between obturacular length and vestimental length (lower) and between obturacular length/width ratio and vestimental length (upper) in *Lamellibrachia satsuma* (closed circle, present study) and *L. barhami* (closed square, data from Jones 1985).

worms were very sensitive to vibration and withdraw into the tube when the tank was shaken. Retraction was very quick.

Among 43 living specimens maintained in the laboratory tank, six died in the first 75 days. Some of the remaining specimens were occasionally removed and dissected to check their condition. About 20 specimens were maintained alive for more than 400 days.

During the maintenance experiment in the laboratory, the worms regenerated their damaged posterior ends. Regenerated opisthosomes were observed at least two months after capture. The posterior ends of tubes were repaired and elongated to attach to a glass bottle which was used as a sinker for a bundle of worm tubes (Fig. 2c). Elongation of the anterior ends of tubes was not observed.

*Spawning.*—Some bottles of specimens were kept in the refrigerator of the research vessel at about 5°C for less than 6 days after their capture before transfer to the rearing tank. In a bottle containing about ten specimens, one released eggs from its tube opening when it was transferred to a tank filled with seawater at about 15°C (room temperature). The newly released eggs were photographed (Fig. 2d) and recorded on videotape. The eggs ranged in diameter from 0.10–0.11 mm ($\bar{X}$ 0.102, $n$ = 11). The eggs were neutrally buoyant in seawater and formed a cloud-like mass drifting in the water, but most eggs transferred to a shallow petri dish floated at the surface. Cleavage of these eggs did not occur in the next five days. Observation was then abandoned.

*Larvae.*—In another bottle kept in the refrigerator, developing embryos were found five days after collection. Most of them were in a swimming, blastula-like stage. These embryos were kept in a small dish at room temperature ranging from 14.0 to 15.5 °C. Most of the embryos developed into trochophore-like larvae (Fig. 2e, f) 0.10 mm in diameter and 0.12–0.13 mm in length ($n$ = 7). The larva had a well-ciliated anterior hemisphere with a prototroch-like ciliated band (Fig. 2e). A telotroch-like ciliated area was also well developed (Fig. 2f). A dark mass observed inside the larva (Fig. 2f) was thought to be comparable with the primitive gut of the early polychaete trochophore, but no blastopore or proctodaeum were observed. The gut-like structure of the larva was completely closed. No larvae had settled after two weeks of observation, when most larvae became inactive.

## Discussion

Kojima et al. (1995) recognized three genetic types of *Lamellibrachia* in the waters around Japan by differences in the amino

acid sequences of the mitochondrial cytochrome c oxidase I. Some *Lamellibrachia* specimens collected from Kagoshima Bay (82–110 m) and those from the Kanasunose Bank of the Nankai Trough (300 m) cluster into one of their types, living shallower than 300 m, which is the species described here as *L. satsuma.* This is thought to be distributed widely on the Southwest coast of Japan in less than 300 m deep. Judging by our preliminary examination of a single specimen from Sagami Bay, another types of *Lamellibrachia* from deeper sites (Kojima et al. 1995) is probably distinguishable from *L. satsuma* in morphological characters such as the body size, tube form, and the number of lamellar sheaths.

As shown in our maintenance experiment, it is not difficult to keep the mouthless worms alive if a suitable chemical energy source such as hydrogen sulfide is supplied. The expanded, blood-red branchiae forming flower-like fans at the top of the tubes may also serve to take up oxygen and carbon dioxide from the water. On the other hand, the source of nitrogen required for their growth or maturation is not yet identified. Since no growth except for some regeneration of posterior parts was observed in reared specimens, a suitable source of nitrogen such as nitrate or dissolved amino acid might have been scarce in the laboratory conditions.

Young et al. (1996) reported observations on the development of two vestimentiferans *Lamellibrachia* sp. and *Escarpia* sp. in the Gulf of Mexico. *Lamellibrachia satsuma* has eggs as large as those of the former but some differences can be seen. The larva of *L. satsuma* has a teminal telotroch-like ciliated area and an internal gut-like dark mass of cells, which were not found in the two species reported by Young et al. (1996). It is not yet clear if these differences are species-specific or not. Our study on the early development of *L. satsuma* is not yet completed and more details will be published elsewhere. The length of the planktonic larval life of *L. satsuma* suggested by the slightly buoyant eggs and a trochophore-like larva able to swim for more than two weeks is enough to explain their distribution in several sites along the Southwest coast of Japan washed by the strong Kuroshio Current. The Kagoshima Bay population of *L. satsuma* might have been formed originally by pioneer larvae released from a neighboring population outside the bay. The larvae might have settled at the active volcanic vents which are thought to have been more numerous and active in the bay during its formative period than at present. The northern part of the bay has been almost closed by the formation of Mt. Sakurajima during 13,000 years (Aramaki & Ui 1966), since the postulated colonization by the pioneer worms.

## Acknowledgments

We thank the captain and crew of R/V *Kaiyo* and R/V *Natsushima,* and the operation team of *Dolphin 3K* for their cooperation and enthusiasm throughout the surveys. Our special thanks are also due to M. Nedachi, K. Oki, and H. Sakamoto of Kagoshima University, J. Ossaka of Tamagawa University, and K. Fujikura of JAMSTEC for their enthusiasm and assistance of the surveys. The manuscript was improved by the careful review and corrections by E. C. Southward of Marine Biological Association, J. L. Norenburg of Smithsonian Institution, and an anonymous reviewer. This work was supported in part by grant-in-aid for the first author from the Ministry of Education, Science, Sports, and Culture, Japan (No. 06839021).

## Literature Cited

Aramaki, S., & T. Ui. 1966. The Aira and Ata pyroclastic flows and related calderas and depressions in southern Kyushu, Japan.—Bulletin of Volcanology 29:29–47.

Danndo, P. R., A. J. Southward, E. C. Southward, D. R. Dixon, A. Crawford, & M. Crawford. 1992. Shipwrecked tube worms.—Nature 356:667.

Hashimoto, J., S. Ohta, K. Fujikura, & T. Miura. 1995. Microdistribution pattern and biogeography of

the hydrothermal vent communities of the Minami-Ensei Knoll in the Mid-Okinawa Trough, Western Pacific.—Deep-Sea Research, Part I, Oceanographic Research Papers 42:577–598.

———, ———, T. Tanaka, H. Hotta, S. Matsuzawa, & H. Sakai. 1989. Deep-sea communities dominated by the giant clam, *Calyptogena soyoae,* along the slope foot of Hatsushima Island, Sagami Bay, Central Japan.—Palaeogeography, Palaeoclimatology, and Palaeoecology 71:179–192.

———, T. Miura, K. Fujikura, & J. Ossaka. 1993. Discovery of vestimentiferan tube-worms in the euphotic zone.—Zoological Science 10:1063–1067.

Jones, M. L. 1985. On the Vestimentifera, new phylum: Six new species, and other taxa, from hydrothermal vents and elsewhere.—Bulletin of the Biological Society of Washington 6:117–158.

Kojima, S., J. Hashimoto, & S. Ohta. 1995. The distribution and the phylogenies of the species of genus *Calyptogena* and those of vestimentiferans around Japan.—JAMSTEC Journal of Deep Sea Research 11:243–248. (In Japanese with English abstract).

———, ———, M. Hasegawa, S. Murata, S. Ohta, H. Seki, & N. Okada. 1993. Close phylogenetic relationship between Vestimentifera (tube worms) and Annelida revealed by the amino acid sequence of elongation factor-1α.—Journal of Molecular Evolution 37:66–70.

Mañé-Garzón, F., & R. Montero. 1985. Sobre una nueva forma de verme tubícola—*Lamellibrachia victori* n. sp. (Vestimentifera)—Proposición de un nuevo phylum: Mesoneurophora.—Revista de Biologia del Uruguay 8:1–28.

Oki, S., & S. Hayasaka. 1978. Geological study on Kagoshima Bay, South Kyushu, Japan. Part IV—A note on the peculiar mode of occurrence of foraminifers in the bottom sediments of the bay-head area.—Report of Faculty of Science, Kagoshima University, in Earth Science and Biology 11:1–11.

Rouse, G. W., & K. Fauchald, 1995. The articulation of annelids.—Zoologica Scripta 24:269–301.

Southward, E. C. 1991. Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-arc Basin (Southwest Pacific Ocean).—Journal of Natural History 25:859–881.

———, & S. V. Galkin, 1997. A new vestimentiferan (Pogonophora: Obturata) from hydrothermal vent fields in the Manus Back-arc (Bismarck Sea), Papua New Guinea, Southwest Pacific Ocean.—Journal of Natural History 31:43–55.

———, V. Tunnicliffe, & M. Black. 1995. Revision of the species of *Ridgeia* from northeast Pacific hydrothermal vents, with a redescription of *Ridgeia piscesae* Jones (Pogonophora: Obturata = Vestimentifera).—Canadian Journal of Zoology 73:282–295.

Suzuki, T., T. Takagi, K. Okuda, T. Furukohri, & S. Ohta. 1989. The deep-sea tube worm hemoglobin: Subunit structure and phylogenetic relationship with annelid hemoglobin.—Zoological Science 6:915–926.

van der Land, J., & A. Nørrevang. 1975. The systematic position of *Lamellibrachia* (Annelida, Vestimentifera).—Zeitschrift für zoologische Systematik und Evolutionsforschung, Sonderheft 1975:86–101.

Webb, M. 1969. *Lamellibrachia barhami,* gen. nov., sp. nov. (Pogonophora), from the northeast Pacific.—Bulletin of Marine Science 19:18–47.

Williams, N. A., D. R. Dixon, E. C. Southward, & P. W. H. Holland. 1993. Molecular evolution and diversification of the vestimentiferan tube worms.—Journal of the Marine Biological Association of the United Kingdom 73:437–452.

Young, C. M., E. Vázquez, A. Metaxas, & P. A. Tyler. 1996. Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps.—Nature 381:514–516.